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EVALUATION OF SWIMMING ABILITY AS A MEANS OF ISLAND INVASION BY SMALL MAMMALS IN COASTAL VIRGINIA

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Abstract

Small mammals were live-trapped on the mainland and on an island located in the southeast corner of Virginia. White-footed mice (*Peromyscus leucopus*) were trapped on the mainland, but not on the island, whereas meadow voles (*Microtus pennsylvanicus*) inhabited both the island and mainland areas located to the south and west of the island. A series of swimming tests was performed on both of these species in both field and laboratory to determine if swimming abilities could be a factor preventing *P. leucopus* from invading the island. Both species of small mammals showed good swimming endurance in water of 30°C, but meadow voles had significantly better swimming endurance in water of 20 and 10°C than did white-footed mice. The pelage of *M. pennsylvanicus* repelled water better in water of 30 and 20°C than did that of *P. leucopus.* The repellent properties of the fur of meadow voles may be due in part to their grooming habits. After being removed from water, meadow voles began grooming more quickly than did white-footed mice. Ninety-five % of *M. pennsylvanicus* tested voluntarily crossed an artificial water barrier, whereas only 50% of *P. leucopus* crossed the barrier of their own volition. When released 200 m from shore, meadow voles swam directly to land; however, only a few white-footed mice could orient toward land from a minimal distance of 50 m from shore. The comparatively poor swimming ability of *P. leucopus* is thought to be an important factor accounting for its meager representation on islands in North America.

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INTRODUCTION

Studies examining the dynamics of small mammals inhabiting islands in North America are relatively common, focusing primarily on species composition. In Canada, most available work on insular populations of small mammals is from eastern provinces (Sutton and Hamilton, 1932; Cameron, 1958; Sheppe, 1965). In the conterminous United States, Marshall (1940) surveyed mammals occupying islands in the Great Salt Lake, Utah, and Daugherty et al. (1978) evaluated mammalian distribution on many islands in Flathead Lake, Montana. Many studies of island populations have been conducted in the Midwest (Dice, 1925; Manville, 1950, 1951; Pruitt, 1951; Beer et al., 1954). More recently, Ozoga and Phillips (1964) and Fall et al. (1968) investigated mammalian population dynamics and distributional patterns on islands in Lake Michigan and western Lake Erie, respectively. Farther east, studies have detailed distribution and abundance of mammals residing on islands in New York state (Hatt, 1928; Werner, 1956; Webb, 1965). Small islands along the coast of eastern United States have served well for investigations of experimental zoogeography (Crowell, 1973; Crowell and Pimm, 1976; Grant, 1970, 1971; Mehlhop and Lynch, 1978).

Surveys of the mammalian constituents of islands located along the coast of Maryland and Virginia are sparse. Paradiso and Handley (1965) provided a checklist of mammals occupying Assateague Island and Dueser et al. (1979) provided information on local distribution and relative abundance of mammals inhabiting nine barrier islands along the Delmarva Peninsula. No published work is available to account for mammals inhabiting the islands of the Back Bay region of coastal Virginia. However, reconnaissance trapping for the present study and trapping conducted by Handley (personal communication) in 1956 revealed that mainland areas had populations of *P. leucopus* and *M. pennsylvanicus,* whereas the largest island in the region (Long Island) supported only *M. pennsylvanicus* and *Oryzomys palustris. Peromyscus leucopus* was not found to occupy Long Island although seemingly suitable habitat existed.

The white-footed mouse and meadow vole are broadly sympatric and widespread in North America. However, the former is absent from most islands throughout its range, whereas the latter is common on islands. This fact suggests that there has been little movement of *P. leucopus* from mainland populations onto islands. Some exceptions include the work of Paradiso and Handley (1965) who found *P. leucopus* to be common on Assateague Island in Virginia. However, this island has been isolated from the mainland for only 50 years, having been formed when hurricane activity created an inlet, separating it from the mainland. Recent connection with the mainland may account for the high number of *P. leucopus* on the island. Other investigators have reported the presence of *P. leucopus* on islands in the Midwest and in Canada (Werner, 1956; Sheppe, 1965; Fall et al., 1968). Water in these areas froze during winter months, providing an avenue for dispersal.

In order to understand more fully a given insular fauna, investigators have evaluated the swimming ability of selected species. To this end, most reports tend to be anecdotal, based on brief encounters with individuals in the field (Orr, 1933; Blair, 1939; Davis, 1942; Teeters, 1945; Fisler, 1961). The swimming ability of cricetid rodents also has been evaluated by employing controlled laboratory studies. Behavioral comparisons, which included swimming within the genus *Peromyscus,* were carried out by King (1961) and King et al. (1968). Getz (1967) measured swimming ability of four species of small mammals and correlated their abilities with habitat selection. A thorough laboratory investigation of swimming of small mammals was conducted by Dagg and Windsor (1972). They observed and filmed swimming of 31 species, and measured gait pattern, speeds, and position in the water. More recently, Evans et al. (1978) performed a comparative study of swimming behavior in eight species of muroid rodents. Esher et al. (1978) recently compared the swimming behavior of rice rats (*O. palustris*) and cotton rats (*Sigmodon hispidus*) and correlated swimming ability with habitat utilization. In the present study, our objective was to test swimming ability both in the field and laboratory of two common species of rodents inhabiting an estuarine embayment region of southeastern Virginia, in order to understand why one species (*M. pennsylvanicus*) has successfully invaded an island and the other (*P. leucopus*) has been unable to do so. An understanding of this local phenomenon may aid in explaining the distribution patterns of these species on islands in North America.

METHODS

This study was conducted in Back Bay National Wildlife Refuge, Virginia Beach, Virginia, located at 36°40′ and 75°55′ on the east coast of Virginia, and is comprised of 1861 ha. The Refuge consists of a shallow bay with two large islands and many smaller ones. In addition, it includes part of the mainland which is a narrow strip of land that separates Sand and Shipps bays (both part of Back Bay proper) from the Atlantic Ocean (Fig. 1). The Refuge was established in 1938 and at that time was largely a salt water estuarine embayment, with abundant eel grass (*Zostera marina*) growing in the bay waters. With the advent of dune management practices a large dune system was established along the coastal line. This dune system caused the bay areas to support a relatively freshwater situation resulting in a profuse growth of milfoil (*Myriophyllum* sp.) during summer months.

The mainland of Back Bay consisted of four distinctive habitat types—sand dunes with adjoining beach area, scrub-brush thickets, marsh, and pine woodland. The principal plant of the dune area was sea oats (*Uniola paniculata*), whereas bayberry (*Myrica

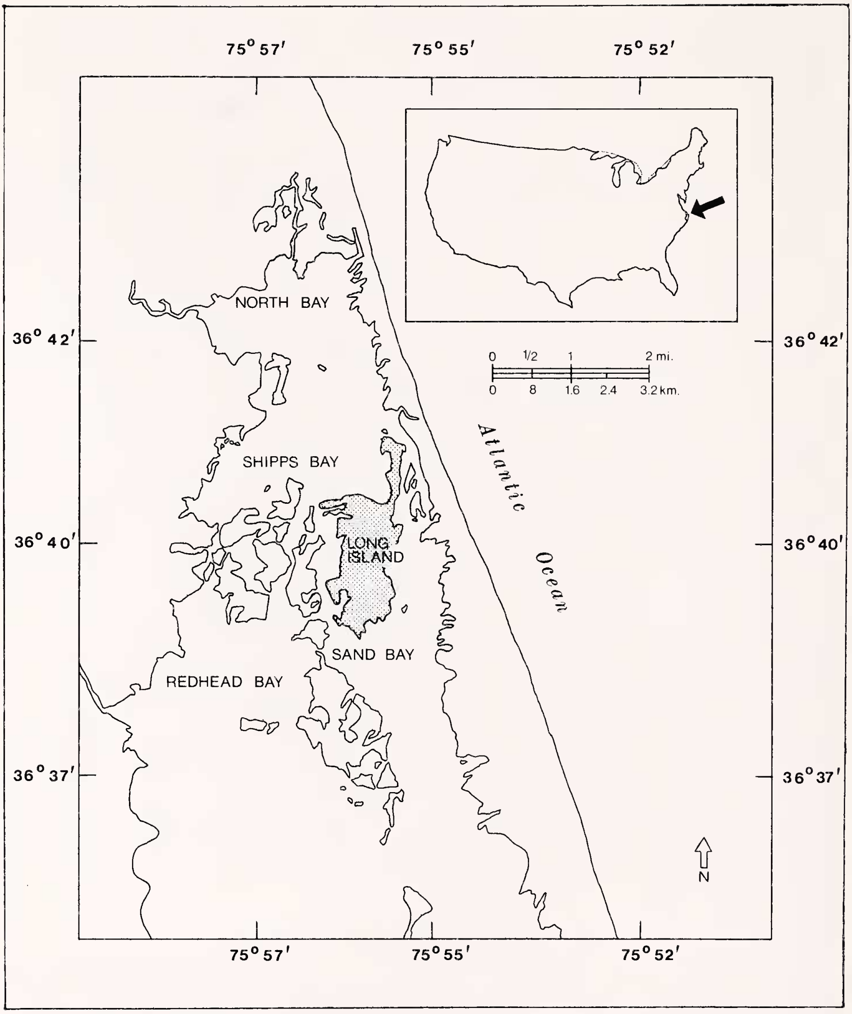

Fig. 1.—Map of Back Bay National Wildlife Refuge showing position of Long Island and surrounding mainland. Inset signifies approximate position of study region along the Atlantic Coast of the United States.

cerifera) and live oak (*Quercus virginiana*) were common in the scrub-brush thickets. Members of the cordgrass family (principally *Spartina* spp.) were abundant in the marsh habitat. Periodic stands of *Juncus roemerianus* and cat-tail (*Typha latifolia*) also contributed to the marsh habitat. Loblolly pine (*Pinus taeda*) was dominant in the pine woodland with intermingling of live oak (*Q. virginiana*). Long Island showed a generally similar floral composition to the mainland. This island (7.6 ha in area) possessed a shrub-brush area, marsh area, and pine woodland community, but instead of a sand dune-beach habitat, it possessed a grass-field community. Also, the pine woodland habitat showed infiltration of hardwood species. Three fields of tall fescue (*Festuca arundinacea*) were present on the island. Prior to 1938, these fields were farmed commercially but currently are managed by the Refuge to provide food for wintering waterfowl. A detailed account of flora of the mainland and Long Island was provided by Carter (1979). The eastern side of Long Island is isolated from the mainland by a channel of 520 to 960 m of water, whereas the western side averaged a distance of 2.73 km from the mainland. Numerous small islands surround Long Island, making the longest uninterrupted water expanse about 160 m. These smaller islands are cordgrass marshes unsuitable for colonization by small mammals. Small mammals were collected for swimming trials from the Back Bay area by employing live-trapping methods. Sherman traps were set along 100 m line transects with two traps per station with a station to station interval of 10 m. Traps were baited with sunflower seeds.

Field Procedures

To determine if swimming abilities may account for the presence of *M. pennsylvanicus* on Long Island and the absence of *P. leucopus* from this island, 10 meadow voles and 10 white-footed mice were tested in the waters of Back Bay. *Oryzomys palustris* (an inhabitant of Long Island) was not tested for it has been demonstrated clearly to be a proficient swimmer (Esher et al., 1978). As a means of measuring swimming distance and orientation, a 200 m line was established radiating from the shoreline of Long Island with markers positioned at 50 m intervals. Animals were introduced into the water initially at 50 m from shore and followed in a boat as they swam. If the animal began to submerge involuntarily or if it successfully reached the shore, it was removed from the water by use of a net. The animal was then released where it was originally captured. If the animal was unsuccessful at reaching land from 50 m, another member of the same species was tested from 25 m and if unsuccessful the trial was conducted at 10 m from shore. If the animal successfully reached shore from 50 m, another member of the same species was tested from 100 m and this sequence was continued until a given animal was unable to orient to land or could not successfully complete the distance. Two members of each species were required to complete a given distance before that species was considered ''acceptable'' at a specified distance. During field trials, the following information was taken: water temperature; water condition (choppy, slightly choppy, calm); position of body in water; type of locomotion employed; pelage condition; distance attempted and completed; length of time in water. Carter (1979) provided a thorough description of each criterion used to evaluate swimming ability.

Laboratory Procedures

Twenty meadow voles and 20 white-footed mice were collected during January 1979 through April 1979 from the Back Bay region. Animals were housed in the laboratory and maintained on a diet of Purina laboratory chow, sunflower seeds, oranges, and water *ad libitum* for the duration of the study.

To determine if animals exhibited the endurance to swim the distance between the mainland and Long Island and how seasonal variation in water temperature affected their performance, swimming bouts were conducted in a 60 by 58 by 30 cm tank for 30 min at three different temperatures (10, 20, 30°C). These temperatures were selected in that they corresponded to the typical temperature regime encountered year-round in the waters of Back Bay. During each test, swimming ability was analyzed by recording the following information: weight before and after swimming; time of swimming bout; grooming characteristics; type of locomotion employed; posture; pelage condition. When possible, the above data were analyzed for significance at the 0.05 confidence level by the Student's *t*-test.

Table 1.—*Mean swimming times (minutes) for* Microtus pennsylvanicus *and* Peromyscus leucopus *in water temperatures of 30°C, 20°C, and 10°C. Sample size was 20 individuals of each species per trial (±S.E.).*

	Microtus pennsylvanicus			*Peromyscus leucopus*		
Sex	30°C	20°C	10°C	30°C	20°C	10°C
Sexes combined	30 (0)	29.5 (0.47)	16.1 (1.61)	30 (0)	26.6 (1.03)	9.5 (0.58)
Males	30 (0)	30 (0.11)	16.6 (1.95)	30 (0)	27.5 (0.85)	10.4 (0.76)
Females	30 (0)	29 (0.67)	16.0 (0.76)	30 (0)	25.8 (1.16)	8.5 (0.36)

In order to assess the degree in which mice and voles voluntarily enter water a wooden test chamber equipped with a water barrier was employed. The test chamber consisted of a plastic-lined trough (260 by 56 by 16 cm) with a platform at each end. A water barrier 200 cm in length and 9 cm deep was located between the platforms. This water barrier made it necessary for small mammals to swim to reach the other platform. The entire apparatus was covered with hardware cloth. The test chamber was modified from that employed by Esher et al. (1978). Testing consisted of removing an animal from its holding cage and placing it into a large Sherman trap (supplied with sunflower seeds and cotton nesting material) which was placed on a platform with the door secured open. On the opposite platform was set another large Sherman trap equipped with the same amount of sunflower seeds and cotton nesting material. Each animal tested was allowed to remain in the chamber no more than 18 h. If the animal was able to swim the water barrier it was trapped on the opposite platform and if not, it was secured from the same platform and returned to the laboratory holding cage. No animals were tested more than once. Results were tested for significance with the Chi-square test.

RESULTS

Directional Orientation

Directional orientation of *M. pennsylvanicus* and *P. leucopus* was tested in the field. In three different sessions, ten individuals of each species were tested. The distances that animals were released from shoreline ranged from 10 to 200 m. With the exception of one meadow vole, all individuals completed swimming trials when tested at varying distances from shore. As expected, both choppy water and lower water temperatures produced slower swimming times and many variables associated with field circumstances complicated exact quantitative analyses. Individual variation made inter- and intraspecific comparisons difficult and therefore only general trends are reported.

Nine out of 10 voles tested swam directly for land as soon as released into the water. At variance to this strong orientation ability was a single individual female that did not reach shore. When released, it initially swam in small circles for 30 sec, then began swimming with the wind, parallel to the island shoreline. Meadow voles were able to reach land from 200 m with little difficulty. Moreover, the route of travel to land was straight with no directional changes.

Table 2.—*The mean weight gain (g) due to water retention in pelage of* Microtus pennsylvanicus *and* Peromyscus leucopus *in water temperatures of 30°C, 20°C, and 10°C. Sample size was 20 individuals of each species per trial (±S.E.). Figures represent the per cent weight gained of the initial body weight.*

Sex	*Microtus pennsylvanicus*			*Peromyscus leucopus*		
	30°C	20°C	10°C	30°C	20°C	10°C
Sexes combined	7.1 (0.94)	8.0 (1.16)	14.1 (1.79)	17.5 (1.45)	12.7 (1.43)	13.4 (0.89)
Males	8.0 (0.96)	9.9 (1.16)	13.2 (0.89)	17.1 (1.36)	10.4 (1.30)	15.9 (2.06)
Females	6.2 (0.92)	6.1 (1.16)	13.6 (0.92)	17.9 (1.54)	14.9 (1.54)	11.8 (1.43)

Results of the field swimming tests for *P. leucopus* contrasted sharply with those of meadow voles. White-footed mice did not perform well in this test as demonstrated by the fact that only two of the 10 mice tested showed positive signs of actually swimming for shore as a means of escape or orientation in the water. Only four mice reached shore from 50 m. However, two of these mice swam in very irregular patterns characterized by swimming in circuitous patterns accompanied by almost fortuitous straight-line orientations toward land. The other two individuals that reached shore from a distance of 50 m did swim continuously on a straight line toward the nearest land mass. Six of the 10 mice tested appeared disoriented, changing their course many times and often swimming in circles. When the first white-footed mouse was tested from 50 m and it was noted that they may only swim in circles, the distance attempted was reduced in order to delimit a particular distance at which all could orient toward land. One individual was released as close as 10 m from land, swam within 7 m of this land mass, and then radically changed direction away from land.

Although field tests lacked rigid quantitative comparisons, work clearly demonstrated the superior ability of meadow voles to orient to land and to endure travel in water of low temperatures characterized by turbulence. In contrast, white-footed mice demonstrated inferior ability to orient and to endure water conditions found naturally in the Back Bay region. In order to refine the field investigation, swimming ability of white-footed mice and meadow voles also was analyzed in the laboratory.

Swimming Endurance

Swimming endurance was tested in the laboratory for meadow voles and white-footed mice at three different temperatures. Testing entailed 30-min swimming trials for 20 animals of each species at temperatures of 30, 20, and 10°C (Table 1).

Microtus pennsylvanicus.—When tested at 30°C all meadow voles swam well for the duration of the testing period. During the trial, voles maintained the dorsal half of their body well above the surface of the water while swimming and floating, and comparatively little energy was expended to maintain this posture in the water. During testing, voles explored the tank by diving beneath the water. As a result of submersion, the pelage took on a glistening appearance due to a layer of air being trapped within the fur. Their eyes were kept open at all times and upon surfacing the pelage was quite dry. A decrease of 10°C in water temperature did not greatly affect swimming endurance of *M. pennsylvanicus*. Only one vole was unable to swim for the 30-min trial period at 20°C. In general, their behavior in water of 20°C was similar to that seen in 30°C. No significant difference was found between mean endurance time for males and females. When tested at 10°C, a greatly reduced swimming ability (endurance) was noted in voles. Only 10% of the animals tested in water of 10°C could withstand immersion for the full 30-min period. Mean swimming time for sexes combined was shorter by about one half in water 10°C than 30°C. Body flotation was similar to that seen in higher water temperatures, however, muscular activity declined resulting in locomotor ataxia. Floating rather than active swimming occurred about 6 min after initiation of trial. As fatigue developed, dipping of the head became common, eventually causing death due to excessive aspiration of water. When symptoms of drowning appeared, animals were removed from water.

Peromyscus leucopus.—Swimming endurance of white-footed mice was good in water of 30°C, all animals completing the 30-min swimming duration (Table 1). White-footed mice commonly floated high in the water although not to the degree seen in voles. Diving was not observed in *P. leucopus* at any time during this study. Swimming duration in water of 20°C was depressed compared to that for trials conducted in water of 30°C. Thirty-five % of animals could not complete the swimming period of 30 min. The mean time for combined sexes was about 3 min less than that for meadow voles at the same temperature. Those mice that completed the entire 30-min swim showed partial paralysis of the hind limbs and moved in jerky, labored actions. As was the case with voles at 10°C, white-footed mice exhibited ataxia resulting in the inability to maintain their noses above the surface of the water. No significant difference was found between mean swimming endurance of male and female mice as compared by Student's *t*-tests. A very low tolerance was seen in white-footed mice when subjected to water of 10°C. Here, the mean endurance time was about 6.5 min shorter than that exhibited by meadow voles at the same temperature. Physical reactions of mice at 10°C were similar to those at 20°C although symptoms occurred earlier in the trial. Once again, mice began imbibing water during final stages of the test. At times during the swim, mice appeared to fall asleep, at which time their noses dipped below the surface of the water. This startled the animals and precipitated increased locomotor activity for a short time.

Comparison between the swimming endurance of meadow voles and white-footed mice revealed that the former exhibited greater endurance. At water of 30°C no significant difference was found on the interspecific level. However, a significant difference ($P \leqslant 0.05$) was found in mean swimming times between the two species in water of 20 and 10°C—*M. pennsylvanicus* showing a longer endurance time than *P. leucopus*.

Weight Dynamics

The weight gained by meadow voles and white-footed mice due to water retention in the fur while in the water for a 30-min trial was measured in the laboratory. Twenty individuals of each species were weighed prior to and following swimming bouts in water of 30, 20, and 10°C (Table 2).

Microtus pennsylvanicus.—The weight of voles before and after 30-min swimming trials was determined and the resulting weight gain due to water retention in the pelage was expressed as a percent gain of the initial body weight. When tested in water of 30°C, voles gained an average of 7.1% of their original body weight due to water retention. The percent of body weight gained ranged from 0.3 to 22%; the two greatest percentage gains were by the two largest voles. One vole weighing 68.6 g gained 16.8% of its original body weight due to water. The second largest vole (60.9 g), gained 22% of its original body weight in water during a 30-min swimming trial. When tested in water of 20°C, voles gained a mean of 8% of their body weight due to water. However, the largest voles did not gain the most weight in water of 20°C. Rather, largest gain was 17.8% of original body weight by a small vole of only 28 g. Percentage of body weight gained due to water retention in water of 10°C ranged from 5.8 to 40% with a mean of 14.1%. In water of 10°C, the mean percentage of weight gained by voles was significantly greater than in water of higher temperatures. This was twice the retention measured for voles in water of 30°C and animals were in water for less than half as long. The largest individual (65.3 g) gained the most weight (40% of initial body weight) from water maintained in the pelage.

Peromyscus leucopus.—As shown in Table 2, white-footed mice gained a mean of 17.5% of their original body weight due to water retention after swimming in water of 30°C for a 30-min trial. Unlike *M. pennsylvanicus,* the largest individuals tested did not gain the most weight during swimming. The percent of weight gained ranged from

6.6 to 28.6%. *Peromyscus leucopus* retained a significantly larger amount of water in its pelage than did *M. pennsylvanicus* during endurance trials in water of 30°C. Swimming trials in water of 20°C resulted in an average of 12.7% gain in weight by white-footed mice during a swimming bout of about 26.5 min. As was the case in water of 30°C, the largest individuals tested did not gain the most weight due to water. The per cent weight gain ranged from 3.6 to 26%, and *P. leucopus* was found to retain a significantly larger amount of water in its pelage than *M. pennsylvanicus* during endurance trials in water of 20°C. Swimming trials for endurance of *P. leucopus* were comparatively short as detailed in Table 1. During a swimming bout in water of 10°C for 9.5 min, mice gained 13.4% of their original body weight due to water—a mean rate of about 0.3 g water/min retained in the pelage during swimming. The percentage of body weight gained due to water ranged from 8.5 to 24.3%. In water of 10°C, *P. leucopus* gained significantly less weight than *M. pennsylvanicus* due to water retention. This difference was due to the fact that *P. leucopus* spent less time in the water (average, 9.5 min) than *M. pennsylvanicus* (average, 16.3 min) giving less time for water retention in the pelage.

Latency before Grooming

The amount of time that passed before an animal began grooming once it was removed from the swimming tank at the conclusion of a trial was referred to as grooming latency time. This experiment dealt only with animals tested in water of 30°C. Latency before grooming was not recorded from swimming trials in water of 20 and 10°C because animals were generally too cold and immobile to groom when removed. Latency times were recorded for 20 *M. pennsylvanicus* and 20 *P. leucopus*.

Microtus pennsylvanicus.—All meadow voles tested began grooming before 3 min following removal from swimming chamber. Grooming latency time ranged from 3 sec to 2 min post-removal. Three individuals initiated grooming 3 sec following removal. The mean time elapsed before grooming occurred was 23.2 sec after removal from the tank following a 30-min swim in water of 30°C.

Peromyscus leucopus.—Only five of the 20 white-footed mice tested began grooming before 3 min post-removal. Others began grooming at various intervals following the 3-min mark. The earliest at which a mouse began to groom was 3 sec post-removal. A mean of about 2.5 min represented the latency before grooming for *P. leucopus*. White-footed mice averaged about 2 min slower than meadow voles with respect to time elapsed before grooming.

Voluntary Crossing of a Water Barrier

To determine whether *M. pennsylvanicus* and *P. leucopus* would voluntarily cross a water barrier to reach an artificial "island," 20 individuals of each species were tested in the laboratory. Ninety-five % of voles tested (19/20) entered the water and swam 200 cm across the water barrier—one female did not complete this trial. Ten females and 10 male meadow voles were tested and no significant difference was found between sexes by employing the Chi-square test. Unlike meadow voles, only 50% of the white-footed mice successfully crossed the water barrier. Eleven males and nine females were tested resulting in successful crossing by seven males and three females. A significantly greater number of males crossed the barrier than did females (χ^2, $P \leqslant 0.05$).

In addition to those behaviors discussed above, Carter (1979) analyzed and compared the following swimming behaviors in *M. pennsylvanicus* and *P. leucopus*: swimming gait; body position in the water; influence of water on pelage condition; diving and swimming beneath the water. Although no discussion will be undertaken at this time, in each test, *M. pennsylvanicus* showed greater refinement of characters adaptive for colonization of insular environments than did *P. leucopus*.

DISCUSSION

Insular mammalian faunas may be established in different ways such as swimming, transport on ice bridges, rafting on pieces of terrestrial debris originating from mainland areas, and transportation by man. In the present study, we have concentrated on detailing the swimming ability of two small mammals as a mode of island invasion. One may visualize an animal's chance of invading an island as being largely determined by its ability to cross a water barrier to reach that island. In order to elucidate the potential for small mammals actively to invade islands completely surrounded by water on a year-round basis, knowledge of their swimming ability is essential.

In order to invade an island other than by chance, it is assumed that an animal must first perceive an offshore land mass and be able to swim toward it, thereby exhibiting directional orientation. Sheppe (1965) reported that *P. leucopus* released 59 m offshore swam toward the shore, and if driven off course soon returned to the original course. White-footed mice released 305 m offshore tended to swim irregularly, frequently changing direction. Sheppe (1965) concluded that mice tested oriented toward shore primarily by visual means. In the present study, *P. leucopus* showed considerable difficulty orienting to land while in the water at distances ranging from 10 to 50 m from land.

No published work is available to document orientation ability in water of *M. pennsylvanicus*; however, its presence on islands in North America is well known (see Grant, 1971, for review). Jackson (1920) found *M. pennsylvanicus* on islands in Lake Superior that were not more than 2.4 km from the mainland. Crissey and Darrow (1949) found meadow voles on Valcour Island in Lake Champlain located about 2 km from shore. More recently, Mehlhop and Lynch (1978) and Dueser et al. (1979) reported *M. pennsylvanicus* from islands in the eastern Chesapeake Bay and Virginia barrier islands, respectively. In the above studies the means employed by meadow voles to invade these islands generally were not known. In the present study, experimental results from field tests indicated that meadow voles showed superior directional orientation in the water with several voles swimming a straight line toward shore from a distance of 200 m. This ability would allow this small mammal the potential to invade islands in the Back Bay region.

Water temperatures of the Back Bay region during summer months averaged approximately 30°C. Laboratory tests of the present study run at this temperature indicated that voles and mice had no difficulty swimming for the 30-min test period. Sheppe (1965), working during summer in Lake Opinicon, Ontario, found channels separating islands from the mainland to be covered by floating mats of algae. *Peromysus leucopus* was found to employ these mats to travel to islands from the mainland. During summer months, the waters of Back Bay were largely covered with a mat of milfoil (except for a 75 to 100 m expanse across the middle of the Bay). Tests conducted in our study confirm that the weight of either *P. leucopus* or *M. pennsylvanicus* could be supported by this mat of vegetation, thus providing a partial route for island invasion. However, the appeal of this route was somewhat compromised by the increased number of predators present in the waters of Back Bay during summer months (that is, large mouth bass, snapping turtles, water snakes, and the cottonmouth).

During spring and autumn water temperatures of Back Bay averaged about 20°C. Laboratory and field tests revealed that voles and mice were stable in their swimming ability at these temperatures; however, the density of milfoil growth was greatly reduced at this time of year thus eliminating the possible utilization of this invasion route to the island.

Water temperature frequently fell below 10°C during winter months in the Back Bay region and for short periods of time ice sheets would develop except in those more central, open waters of the Bay. During this time (generally not more than one month in duration) small mammals could walk out on the ice and swim across an expanse of open water to another land-connected sheet of ice. However, our laboratory experiments showed that small mammals demonstrated lowered survival when tested in water approximating winter conditions. Esher et al. (1978) reported that most individuals of *S. hispidus* and *O. palustris* showed effects of cold exposure when tested in water baths of 15°C for 40 min—many cotton rats were incapacitated upon removal. Getz (1967) tested *P. leucopus* and *M. pennsylvanicus* in water of 15°C and noted that they swam an average of only 2.4 and 2.8 min, respectively, before exhaustion. Results of our study indicate that survival time of *P. leucopus* and *M. pennsylvanicus* was longer in water of 10°C than those reported by Getz (1967). Attempts by small mammals to traverse bodies of water in Back Bay during mid-winter surely would result in high mortality.

The superior swimming ability exhibited by meadow voles in the present study was due partially to the water repellent and insulative qualities of their fur. Small mammals are known to lose heat rapidly in cold water due to neuromuscular depression which adversely affects swimming capacity (Wilber, 1959; Wilber and Hunn, 1960; Wilber and Weidenbacher, 1961; Sealander and Guess, 1970; Esher et al., 1978). Dry fur possesses superior insulative qualities and conducts heat at a slower rate than does wet fur (Scholander et al., 1950). A dry pelage also increases the buoyancy of an animal, by more readily trapping air between the hairs (Dagg and Windsor, 1972). Esher et al. (1978) indicated that the superior endurance of *O. palustris* over that of *S. hispidus* was due partially to the greater ability of the fur of the former to repel water, thus increasing buoyancy. In the present study, *M. pennyslvanicus* was a more accomplished swimmer than *P. leucopus,* in part due to its ability to maintain a comparatively dry pelage causing the animal to float easily in the water. The pelage of *M. pennsylvanicus* was very dense and well-groomed (grooming was initiated about 20 sec following removal from water). In contrast, the pelage of *P. leucopus* was not as dense as that of *M. pennsylvanicus,* and the former did not initiate grooming as quickly following removal from water as the latter.

The ability to dive and swim underwater has been observed in *O. palustris* (Esher et al., 1978), *Microtus californicus* (Fisler, 1961), and to a lesser degree in *M. pennsylvanicus* (Blair, 1939). Because these species occupy marshy habitats, this aquatic behavior may be adaptive in habitat utilization and colonization. In our study meadow voles commonly dove and swam underwater in both laboratory and field. During the period of submersion, eyes were kept open facilitating orientation. In sharp contrast, when tested under similar circumstances, the white-footed mouse was never observed to dive or swim underwater.

If small mammals were to invade an island actively they normally would enter the water of their own volition. Blair (1939) reported that

M. pennsylvanicus entered and successfully swam across a stream in Michigan and Sheppe (1965) found *P. leucopus* voluntarily to cross water barriers in order to return to their "home" islands when released on "foreign" islands nearby. The distance crossed by mice was small (average 38 m). Experiments with *S. hispidus* and *O. palustris* (Esher et al., 1978) showed that 74% of cotton rats tested voluntarily swam a 200 cm water barrier and all rice rats tested crossed this barrier. Getz (1967) reported that when *P. leucopus* was forced to swim to a feeding station which it previously had been able to walk to, the mice made an average of 31.1% fewer visits to the station, indicating a reluctance to swim. However, under the same circumstances, *M. pennsylvanicus* averaged only a 3.4% reduction in visits to the station. In the present study, we found that *M. pennsylvanicus* successfully crossed a water barrier in 95% of the trials, whereas *P. leucopus* successfully crossed the barrier in only 50% of the trials. These results are in agreement with the trend of voluntary crossing of a water barrier by *P. leucopus* and *M. pennsylvanicus* reported above.

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